Temporal dynamics of the recruitment of glass eels in two valleys of French Polynesia (Tahiti and Moorea Islands)

by

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Abstract. – Glass eels were sampled in two estuaries of French Polynesia (Tahiti and Moorea islands) from 2009 to 2017. Three species were identified by morphological measurements (*Anguilla marmorata*, *A. megastoma* and *A. obscura)*. Our results revealed a difference in the species composition between Moorea and Tahiti. The recruitment of eels is seasonal and occurs between November and March during the rainy season, with peaks in December and January. The recruitment size of glass eels was analyzed for the three species. We found a difference between the sizes at recruitment between Tahiti and Moorea. Overall, using a negative binomial GLM, we show that rainfalls, waves' direction, light and temperature were key factors for glass eel recruitment in French Polynesia.

Résumé. – Dynamique temporelle du recrutement des civelles dans deux vallées de la Polynésie française (Tahiti et Moorea).

Les civelles ont été échantillonnées dans deux estuaires de la Polynésie française dans les îles Tahiti et Moorea, de 2009 à 2017. Trois espèces ont été identifiées par des mesures morphologiques (*A. marmorata, A. megastoma* et *A. obscura*). Nos résultats montrent qu'il y a une différence de composition d'espèces entre Tahiti et Moorea. Notre résultat principal montre que le recrutement des anguilles en Polynésie française est saisonnier et se passe entre novembre et mars pendant la saison des pluies avec un pic de recrutement en décembre et janvier. La taille au recrutement a été comparée pour les trois espèces entre Tahiti et Moorea. Enfin, un modèle multiparamètre nous a permis de montrer que les précipitations, la direction des vagues, la luminosité et la température étaient des facteurs clés du recrutement des civelles en Polynésie française.

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INTRODUCTION

Freshwater eels are widely distributed throughout the world, with 19 species and subspecies of the genus *Anguilla* recognized (Ege, 1939; Watanabe *et al.*, 2004, Watanabe *et al.,* 2009). Eels are unequally distributed with most species present in the tropical regions while a minority of species live in the temperate regions and are absent of the eastern part of the Pacific Ocean and of the South of the Atlantic Ocean (Watanabe, 2003).

Eels are catadromous species that migrate between freshwater habitats and their breeding grounds in the open ocean (Tesch, 2003), where adult eels die after spawning. Egg hatch and release leaf-like larvae called leptocephali. Schmidt (1922) was the first to partially solve the mystery of breeding at sea by capturing leptocephalic larvae of the two species of Atlantic eels *Anguilla anguilla* and *A. rostrata* close to the Sargasso Sea. More recently, the spawning ground was also discovered for *A. japonica* (Tsukamoto, 1992). For all other species, the spawning area is either hypothetical or totally unknown. After several weeks in the ocean, swimming or drifting with oceanic currents, the leptocephali arrive near the continental shelf, and undergo their first metamorphosis in transparent glass eels and enter the freshwater habitat. As soon as they enter freshwater, they get pigmented and reach the yellow eel stage (immature adults). After several years, a proportion of the population metamorphoses into silver eels (mature adults) and start their downstream migration back to the ocean in the place where they were born and complete their life cycle.

Among all eel species, four of them have been reported as commercially exploited in FAO statistics (FAO, 2009), the European eel (*A. anguilla* (Linnaeus, 1758)), the Japanese eel (*A. japonica* Temminck & Schlegel, 1846), the American eel (*A. rostrata* (Lesueur, 1817)) and the short-finned eel (*A. australis* Richardson, 1841). Unfortunately,

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most eel populations are facing a drastic decline for almost 40 years (Casselman and Cairns, 2009) due to numerous factors, including fishing pressure (Dekker, 2004), loss of habitat (McCleave, 2001), global changing ocean conditions (Tsukamoto *et al*., 2009), pathogens (Palstra *et al*., 2007; Fazio *et al*., 2012) and pollution (Van Ginneken *et al*., 2009). Recently, these species have been classified as respectively “Critically Endangered” (*A. anguilla*) and “Endangered” (*A. japonica* and *A. rostrata*) on the IUCN Red List (Hoffmann *et al*., 2010; Jacoby and Gollock, 2014a, b). The stock of the European eel has been described as outside safe biological limits from 1999 by ICES. A European regulation to restore the stock has been implemented by European Union and a trade ban has been implemented by CITES scientific authority since 2010 after the species was listed on Appendix II of the Convention of International Trade of Endangered Species on 2009 (CITES, 2017).

If the life cycle of temperate eels is relatively well known because of the necessity to manage the stocks of exploited populations (Righton *et al.,* 2016), very little is known about the biology and the ecology of the three species found in rivers of French Polynesia. Three eel species are known to occur in French Polynesia (Marquet and Galzin, 1991): the giant mottled eel (*A. marmorata* Quoy & Gaimard, 1824), the Polynesian longfinned eel (*A. megastoma* Kaup, 1856) and the Pacific shortfinned eel (*A. obscura* Günther, 1872). The mottled eel, *A. marmorata*, is the most widely distributed species with an Indo-Pacific distribution from the South African coast in the west to the Far East of French Polynesia. The two other species are restricted to the southwest Pacific region and have been classified as Data Deficient by IUCN (Jacoby *et al.,* 2014). In the Polynesian triangle, eels are often considered as sacred and associated with legends and traditions linked with the creation of life. A population genetic study suspected the existence of at least four populations of *A. marmorata*, from different spawning sites, two in the North Pacific and one or more in the North-Western Pacific and Indian Ocean (Minegishi *et al.,* 2008). This result supports the local panmixia hypothesis suspected in studies conducted in Reunion Island (Robinet *et al*., 2007). But, many grey areas still exist on the life cycle of this species since only one spawning area has been identified to date (Miller *et al.,* 2002; Tsukamoto *et al*., 2011). Data on the two other species are by far even less abundant and the genetic status of *A. megastoma* and *A. obscura* is still unclear (Watanabe *et al*., 2011). Even more essential, very little information is available on the life cycle of these eels and, for example, the recruitment mechanisms or the outmigration period remain unknown (Marquet, 1987, 1988; Budimawan & Lecomte-Finiger, 2005). Finally, as a consequence of the protected status of the three commercially important species, there is a risk of a modification of the trade relationships and demand on tropical eels may increase. There is a disagreement in America on the status of the eel, so far it has not been listed continent wide as endangered because in the southern part, the diminution seems much less important than in the St Lawrence River (Canada). So the American eel is not listed as a CITES species and trade for glass eel has increased.

This article aims to provide new insights on the life cycle of the eel species present in French Polynesia and especially

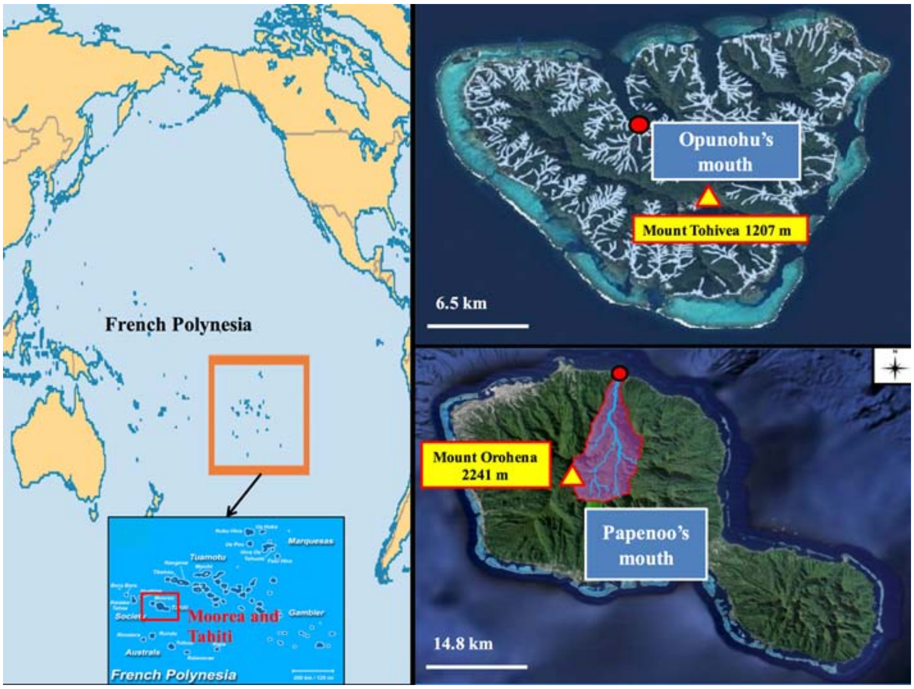

Figure 1. – Location of Opunohu’s mouth in Moorea Island and Papenoo’s mouth in Tahiti Island.

deals with the dynamics of the recruitment of glass eels in two islands, Tahiti and Moorea. The main goal was to capture glass eel entering the river mouth in order to assess species composition, arrival size and the annual temporality according to certain climatic factors.

MATERIALS AND METHODS

Glass eels were collected on the two main islands of French Polynesia using a fyke net (1 m high, 20 m long, 35 cm diameter at the entrance, 4 cm diameter at the end and a mesh size of 1 mm). Samples were done on the island of Moorea, Society archipelago, French Polynesia, in the estuary of the Opunohu River in Opunohu Bay (17°51879'S, 149°85022'W) and on the island of Tahiti, Society archipelago, French Polynesia, in the estuary of the Vaituoru River (17°51356'S, 149°42204'W) in the largest valley of the island (Papenoo valley with almost 90 km^2 surface) (Fig. 1). The collection period in Moorea was punctual, it was made during the months of December and January from 2009 to 2016 with a break for the period of 2012-2013 due to technical problems. The collection period was regular in Tahiti where the net was laid every month from December 2014 until July 2017. For the two islands, glass eels were collected once a day, every morning, but some days are missing because heavy currents and floods during the rainy seasons have made it impossible to leave the net or rendered the collection of samples hazardous. The mean Catch Per Unit Effort (CPUE) was calculated for each period in the two islands by calculating the ratio of the number of glass eels caught per period to the total number of days of capture per period.

The fishes were brought alive to the laboratory, anaesthetized with clove oil and observed under a binocular-dissecting microscope for identification. Individual eels were measured to the nearest mm (total length (TL), predorsal fin insertion length (DL) and preanal fin insertion length (AL), in mm). Eel species identification was done following Ege (1939), considering the coloration of the back and the ratio between the anterior end of the anal (AL) and the dorsal (DL) fins and total body length (TL; ratio = [(AL – DL) / TL) × 100]). This ratio is particularly important for small fishes or when coloration is not clear enough. It allows differentiation between shortfin species (ratio < 8% for *A. obscura*) and longfin species (ratio [8-13%] for *A. megastoma* and >14% for *A. marmorata*) (Ege, 1939; Tesch, 2003; Watanabe *et al*., 2004). Glass eels with ratio [13-14%] were defined as *A. megastoma*/*A. marmorata*. Number of captured eels from each species was recorded daily.

Each fishing day, temperature (in °C), rainfalls (in mm), lunar phase, swell direction and height (in m) and wind direction and speed (in knots) were recorded. Air temperature and rainfalls were recorded from the Opunohu weather station (17°51880'S, 149°84962'W) for the island of Moorea, and from the weather station in the Papenoo valley (17°51392'S, 149°84834'W) for the island of Tahiti. Swell height and direction and wind speed and direction were reported from WindGURU weather forecasting website (https://www.windguru.cz/62510 for Moorea and https://www.windguru.cz/208784 for the Papenoo estuary). For all of these variables, except for rainfalls, we used a daily mean for statistical analyses. Lunar phase was recorded on website (http://kalender-365.de/). For statistical analysis, lunar phase was transformed in numbers with 0 for the new moon, negative values for days before the new moon and positive values for days after the new moon.

Statistical analyses were performed using the R software (R Development Core Team, 2007). The effect of each environmental variable was tested on glass eel recruitment. Because our data were not normally distributed (Shapiro-Wilk test, p-value < 0.0001 for all variables except temperature and windspeed), they were normalized using Arcsin function and we chose to implement a Generalized Linear Model following a negative binomial distribution (Wajnberg, 2011). The model was built using the number of captured glass eels as the response variable and environmental variables as explanatory factors. Data were analyzed separately for each Island, and using both all species together and a separate model for each species.

RESULTS

Annual monitoring of glass eel recruitment

The recruitment of glass eels in French Polynesia is seasonal and occurs from November to March (Fig. 2). On Moorea Island, 7946 glass eels were collected during 210 days of fishing. Maximum catch was 4000 glass eels in one day (11 Jan. 2016). Mean Catch Per Unit Effort (CPUE) was 44.6 eels/night with a minimum value in 2009-2010 (CPUE = 6.8 eels/night) and a maximum value in 2015-2016 (CPUE = 313.3 eels/night). CPUE was 34.8 eels/night in 2013-2014. CPUE was 8.7 eels/night in 2014-2015. On Tahiti Island, we collected 6311 glass eels spread over 395 fishing days with a peak in January for each year. Maximum catch was 276 glass eels in one day (17 Jan. 2015). Mean CPUE was 31.9 eels/night with a minimum value in 2014-2015 (CPUE = 28.4 eels/night) and a maximum value in 2016-2017 (CPUE = 40.7 eels/night). CPUE was 29.3 eels/night in 2015-2016.

The three species recruited about the same time seasonally, between November and March, with a peak in December at Moorea and in January at Tahiti (Fig. 3).

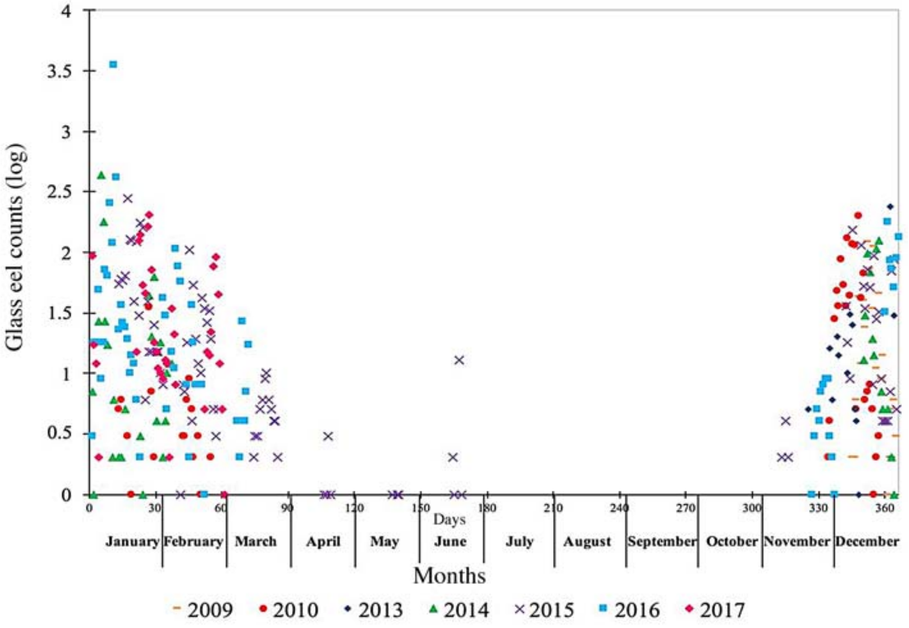

Figure 2. – Annual monitoring of glass eels recruitment in the Opunohu River on the Moorea Island and in the Vaituoru River on the Tahiti Island per year, given in number of specimens caught per day.

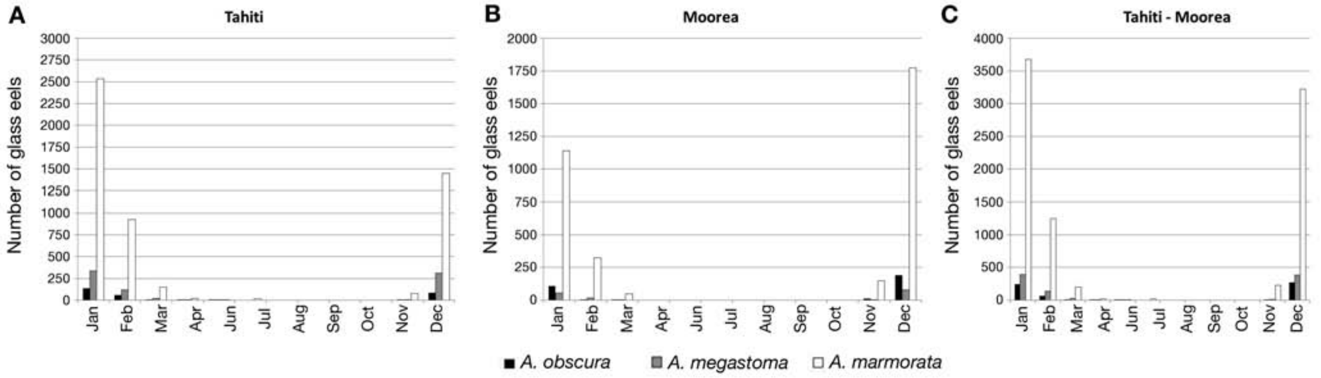

Figure 3. – Annual monitoring of glass eels recruitment for each of the three species in: **A**: Moorea; **B**: Tahiti; **C**: Moorea and Tahiti, given in number of specimens per month.

Species composition

The proportion of each species in our sample varied depending on the year (Fig. 4). However, globally, *A. marmorata* was by far the more abundant species with a mean of 86.5% of all collected eels both in Moorea and Tahiti. *A. megastoma* and *A. obscura* were much less present with a percentage below 10% for each species (7.1% and 6.4%, respectively).

Variations in size

A significant difference was observed in the total length of the three eels species between Moorea and Tahiti. Glass eels from Moorea were larger than those collected in Tahiti (Fig. 5). Mean sizes of each species varied between Moorea and Tahiti. *A. megastoma* was found to be the largest species at recruitment (n = 153; mean = 51.83 ± 1.97 mm in Moorea and n = 795; mean = 48.29 ± 1.97 mm in Tahiti), followed by *A. marmorata* (n = 3430; mean = 51.04 ± 1.76 mm in Moorea and n = 5168; mean = 47.50 ± 1.84 mm in Tahiti) and *A. obscura* was the smallest (n = 317; mean = 49.41 ± 1.78 mm in Moorea and n = 289; mean = 47.07 ± 1.93 mm in Tahiti).

Environmental variables

Using the negative binomial approach, we set up a multifactorial model that took into account the explanatory variables. The basic model was the following one: glass eels count according to the different quantitative variables such as temperature, rainfalls, moon phase, swell height, cloud cover, wind speed, wave direction (WVD) and wind direction (WDD). We applied the same model for each species (Tab. I) except in Moorea because there were not enough data and date were irregular.

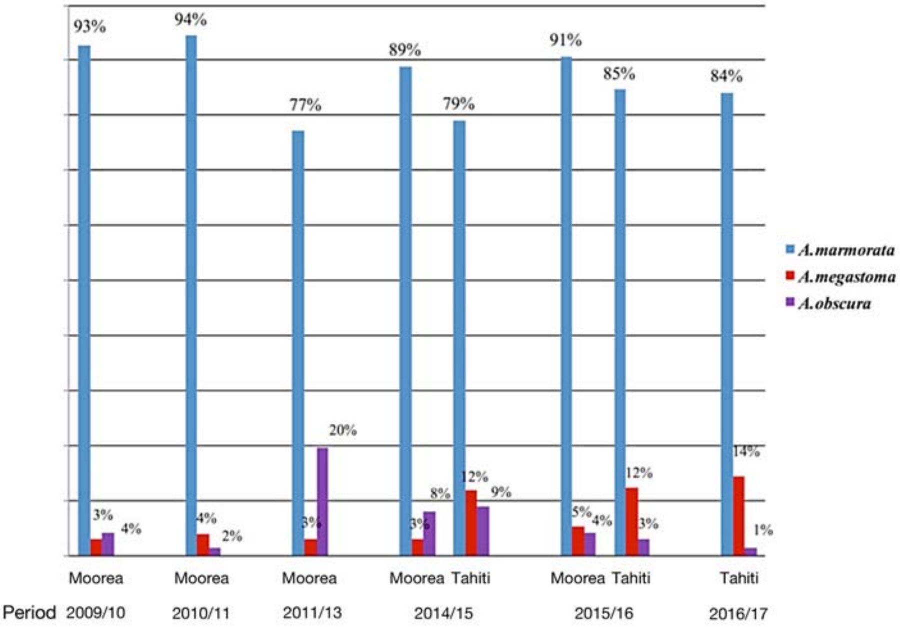

Figure 4. – Composition of the recruitment of *Anguilla* species from Moorea and Tahiti Islands given in percent; * test chi^2, p-value < 0.001.

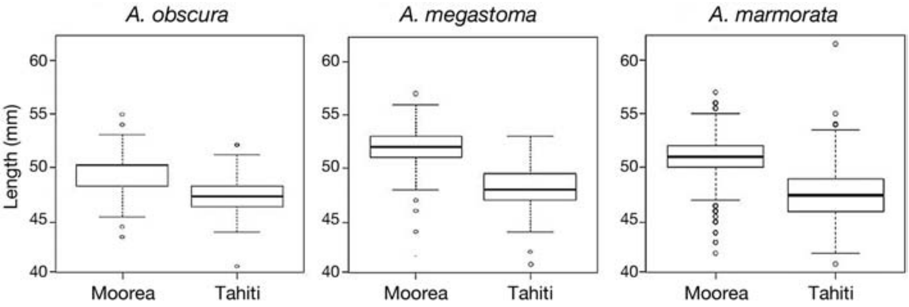

Figure 5. – Mean length (in mm) of the glass eel specimens at recruitment, for the three species in Moorea and Tahiti islands; * test chi^2, p-value < 0.001.

Table I. – Results of ANCOVA on entry-level Generalized Linear Model in Tahiti.

	Tahiti							
Variables	All species		*A. obscura*		*A. megastoma*		*A. marmorata*	
	Effect variables	p-value	Effect variables	p-value	Effect variables	p-value	Effect variables	p-value
Rainfall	0.017 positive	**3.9e-07 *****	0.01	0.173	0.015 positive	**0.0005 *****	0.017 positive	**2,4e-07 *****
Theta(cosmoon)	4.237	0,131	2.05	0.748	2.665	0.491	4.484	0.106
Theta(sinmoon)	–3.542	0,269	0.011	0.999	-1.264	0.776	–3.929	0.215
Temperature	0.387 positive	**0.023 ***	0.54	0.168	0.598 positive	**0.018 ***	0.318 positive	**0,059 .**
Windspeed	–0.07	0,203	-0.242 negative	**0.048 ***	–0.062	0.407	–0.073	0.177
Swellheight	–0.372	0,221	1.054	0.119	-0.099	0.807	–0.409	0.173
Cloudcover	0.007 positive	**0.038 ***	0.005	0.491	0.012 positive	**0.007 ****	0.006 positive	**0,073 .**
Theta(cosWVD)	0.461 positive	**0.003 ****	0.283	0.422	0.606 positive	**0.005 ****	0.459 positive	**0,003 ****
Theta(sinWVD)	0.1	0,547	0.811 positive	**0.032 ***	–0.055	0.807	0.068	0.676
Theta(cosWDD)	–0.119	0,489	-0.458	0.247	-0.219	0.363	–0.118	0.49
Theta(sinWDD)	0.328 positive	**0.035 ***	0.074	0.832	0.166	0.434	0.374 positive	**0.015 ***
Degrees of Freedom	205		205		205		205	
AIC	1689		479		846		1618	
Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1								

For Tahiti, rainfall (p-value = 0.001), wave direction (p-value = 0.003), cloud cover (p-value = 0.038), wind direction (p-value = 0.035) and temperature (p-value = 0.023) had a significant influence on the glass eel recruitment (Tab. I). The model shows that rainfall, temperature, cloud cover and wave direction have a positive effect and wind speed and swell height have a negative effect on the number of eels recruitment.

In Tahiti, glass eels recruitment is significantly influenced by rainfalls (p-value = 0.0005 for *A. megastoma* and p-value < 0.0001 for *A. marmorata*), temperature (p-value = 0.018 for *A. megastoma* and p-value = 0.059 for *A. marmorata*), cloud cover (p-value = 0.007 for *A. megastoma* and p-value = 0.073 for *A. marmorata*) and theta(cosWVD) (p-value = 0.005 for *A. megastoma* and p-value = 0.003 for *A. marmorata*). Theta(sinWDD) (p-value = 0.015) had a significant effect only on the recruitment of *A. marmorata*, while the recruitment of *A. obscura* was significantly influenced by windspeed (p-value = 0.048) and theta(sinWVD) (p-value = 0.032). Theta was used for a cyclic transformation of lunar phase, waves direction and wind direction.

DISCUSSION

Since Marquet (1988), this study is the first one to investigate the recruitment of glass eels of the three Polynesian eel species *A. marmorata*, *A. megastoma* and *A. obscura* in two islands of Society archipelago.

The three species known in French Polynesia, *A. marmorata*, *A. megastoma* and *A. obscura*, have been sampled in the Opunohu River and Vaituoru River. Nevertheless, morphological identification based on fin ratios did not allow us to identify all the specimens collected because of overlapping ratios. Other parameters must be taken into account (number of vertebrae, pigmentation stage…) and a molecular identification is needed for species identification. However, the aim of the study was to establish the dynamic of eel recruitment in French Polynesia and our results provide evidence of the seasonal recruitment for the three eel species between November and March during the wet season, with a clear peak of recruitment between December and February. This result supports the hypotheses of a seasonal recruitment generally observed for other species (Harrison *et al*., 2014). However, our results is in opposite with the previous hypothesis suggesting that tropical eels recruit all year long (Marquet and Galzin, 1991). This result is also in contradiction with the pattern detected by Sugeha in Indonesia (Sugeha *et al.,* 2001; Sugeha, 2011) where an all year-long recruitment is observed. Even if the pigmentation stage was not specifically established in this work, all specimens examined during this study were in the early glass eel pigmentation stages, indicating that they probably recruit to the Opunohu River and Vaituoru River relatively soon after metamorphosis. In Europe, the metamorphosis of leptocephali *A. anguilla* occurs when glass eels arrive on the continental shelf or close to it (Harrison *et al.,* 2014). Because of the structure of seabed near Polynesian islands, *i.e.* very deep, we can imagine that metamorphosis into glass eel occurred when freshwater influence is detected or when sea bottom is higher.

The observed proportion of glass eel at recruitment seemed to be similar to the proportion of adult eels observed in rivers (Marquet, 1987; unpubl. data). *A. marmorata* is by far the most abundant species (85% of the catches and more) in the two islands. This proportion seems to reflect the proportion of yellow eels in the rivers because *A. marmorata* is ubiquitous and colonizes the entire river while *A. obscura* colonizes the bottom and *A. megastoma* the upper valley. Interestingly, we observed a low proportion of *A. obscura* in Tahiti (around 4%) compared to Moorea (around 9%) and a low proportion of *A. megastoma* in Moorea (around 3%) compared to Tahiti (around 12%). A link between available habitats and recruitment strength is presumed, given that Tahiti is twice as high as Moorea; it seems logical that *A. obscura* recruits more in Moorea and *A. megastoma* in Tahiti.

After looking at the annual variation, we looked at the monthly one, with regard to the moon phase. Our results underlined a great influence of lunar cycle, as several previous studies did, both on temperate and tropical species (Sugeha *et al*., 2001; Adam *et al*., 2008; Harrison *et al*., 2014). Our results show an increase of glass eel catches during the new moon phase and a lower catch during the full moon. This result was independent of the tidal amplitude during both periods. This could be explained by the effect of the lunar phase on light intensity and the fact that glass eels are known to be lucifugous, hence highly influenced by light levels (Fontaine, 1950). It is then possible that in absence of other favourable environmental conditions (cloud cover or water turbidity for example), glass eels prefer to remain buried in the substrate during the full moon instead of migrating when the light may facilitate the predation. In other studies, there is a strong influence of the moon phase on the recruitment of temperate and tropical species (Marquet, 1988; De Casamajor, 2001; Sugeha *et al.,* 2001; Robinet *et al.,* 2007; Harrison et *al.,* 2014) but not in this study. This can be explained because the capture of glass eels was only practically during the period of the new moon.

In temperate regions, temperature is a factor that may affect glass eel migration, especially as a reduction of temperature may reduce eel activity and impair the migration (Harrison *et al*., 2014). In the tropical regions like French Polynesia, the temperature variation throughout the year is reduced and higher temperatures are usually associated with the dry season. In our study, we also found a significant influence of the temperature on glass eel recruitment. It supposes that it is possible that the beginning of the recruitment season (in November) is associated with an increase of temperature in rivers.

We also noticed that *A. obscura* was the smallest species and *A. megastoma* the largest. The tropical species were smaller than the temperate species: 10 to 20 mm less for the three Polynesian species compared to *A. anguilla* the European eel (De Casamajor *et al.,* 2001). It is usually admitted that the length of glass eels is proportional to the distance between the recruitment zone and the spawning areas (Marquet, 1992; Aoyama *et al.,* 2003; Minegeshi *et al.,* 2008). Thereafter, our results confirmed that the spawning area of the eels collected in French Polynesia might be close to the Islands and that the one of *A. obscura* is probably even closer. Studies on the otoliths have to be done in different Pacific islands in order to gain more precise information.

According to our results, recruitment would also be influenced by other parameters such as rainfalls, temperature, cloud cover, wind direction and wave direction. A supply of freshwater associated with an increase in flow of the river would therefore favour the arrival of glass eels in the Vaituoru River, this could be different in Moorea in the Opunohu River as glass eels have to cross a 2 km long bay before reaching the river mouth. This could explain why, even during the heavy rains of the wet season, freshwater influence is lower in Moorea.

In tropical areas like French Polynesia, the tidal effect is limited compared to temperate areas. Our results revealed that swell height was not the most important factor in glass eel recruitment. We hypothesized that swell height facilitates glass eel progression and waves should push glass eels in the estuary. Our results showed that instead of the swell height, the swell direction is much more important. This could give some information on the direction glass eels are coming from. In order to confirm that, it would be interesting to obtain samples from rivers located at different orientations.

PERSPECTIVES

After this first annual survey of glass eels in French Polynesia, it sounds relevant to continue the survey of glass eels over the long term, especially in the context of global change and because French Polynesia is in the easternmost part of South Pacific eel distribution. Moreover, the monitoring should be extended to other archipelagos such as Marquesas and to other rivers of Tahiti in order to estimate the impact of hydroelectric power stations on glass eel recruitment. Finally, the recruitment of other diadromous species remains unknown despite conservation and biological interest. As such as the gobid endemic species in French Polynesia should be surveyed.

The control of the recruitment of glass eels is complex and includes behavioural, environmental and hydrodynamic factors. Applying a same model of glass eel recruitment across different estuaries in French Polynesia can be problematic due to variations in environmental conditions. Thus, to understand the entire recruitment process and produce a reliable estimation of the yearly recruitment of glass eels to the adult population, recruitment studies on a site-by-site basis are required to fully elucidate temporal and spatial distribution patterns.

Finally, considering the decrease in temperate eel species and the regulation rules imposed by European community and other international NGOs (UICN, CI, etc.) on the three main species commercially exploited, it remains crucial to accumulate information on the life cycle of tropical eels.

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